



*Patterns of
genetic variation in*

**SUGAR
MAPLE**

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PATTERNS OF GENETIC VARIATION IN SUGAR MAPLE

HOWARD B. KRIEBEL¹

INTRODUCTION

Sugar maple ranks high among eastern North American hardwoods in economic importance. In addition to having desirable wood properties for lumber and specialty products, it is the only important source of maple syrup and maple sugar, and is an excellent shade tree.

A study of racial variation in sugar maple was started at the Ohio Agricultural Experiment Station in 1953. The experiments were designed to reveal heritable differences in survival, growth rate, period of growth, endurance of climatic extremes, tree form, and other measurable characteristics.

A practical objective of the study is the eventual replacement of "run-of-the-mill" nursery stock with seedlings grown from seed of known origin, having known favorable combinations of characteristics of growth and adaptability. For example, a drought-hardy race might be used to extend the range of sugar maple in Ohio to sites on which it does not grow naturally. Selection for high growth rate, good stem form, and high sugar content are some other possibilities. Controlled crossing of selected trees follows selection and can produce trees with new and improved genetic combinations.

Much of the information gathered in the past on racial variation in sugar maple has been obtained from biometric studies of leaf variation. This type of variation, however, is not necessarily associated with other types which influence survival and growth responses. The latter are of more direct concern in forestry.

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This paper is concerned with studies made over a two-year period, with some supplementary third-year evaluations. It includes studies of small trees grown from seed and studies of trees a few years old transplanted from their native localities to an experimental plantation at Wooster, Ohio.

REVIEW OF PREVIOUS STUDIES

Geographic and Climatic Patterns of Tree Variation

The fundamental relationships between geography, climate, and genetic differentiation have proved to be common to many species of deciduous and coniferous forest trees. This knowledge is therefore relevant to a study of sugar maple, a species which has not previously been subjected to this type of study.

The literature on the subject of tree races is extensive, although much of the early experimental evidence was derived from a comparatively small number of species. A number of writers have presented general discussions of basic principles, including Engler (1905), Langlet (1936) and Dorman (1952). The very brief discussion which follows is taken from the author's collation of the literature (1956). It summarizes some characteristics of variation in growth rate and phenology, gross morphology, and adaptability to the environment.

Stem form is usually straighter among trees from northern seed sources (Vilmorin 1862, Dengler 1935). High elevation of seed origin has an effect similar to high latitude on tree form (Engler 1913, Burger 1931). Most of the evidence to date has been obtained from studies of coniferous species.

Trees planted far south of their original source normally grow more slowly than either native trees or trees grown to the north of their original localities. Likewise, trees from higher elevations than the test site grow slowly in comparison with those from equal or lower elevations (Cieslar 1923, Burger 1941). This has been found to be typical of a wide variety of tree species, including pines, larches, oaks, and maples. A southern race growing in a northern locality will sometimes outgrow the native trees of the same species, although climatic and biotic factors limit the distance which southern trees can advantageously be moved to the north (Heikinheimo 1949).

Nearly every species with a wide latitudinal range shows variation in winter hardiness. In a given locality, northern trees are more hardy than southern trees, and trees from high elevation are more hardy than

trees from low elevations (Langlet 1937). Southern trees continue growth late into the fall and are injured by fall frosts. On the other hand, within a species ranging far to the north, northern trees growing far south of their original locality start growth early in the spring and may be injured by late frosts. This has been reported by Heikinheimo (1949), for example, as a characteristic of Norway spruce.

Relatively little information is available in the literature on the relationship of summer hardiness to provenance in forest trees. Racial differences in drought resistance have been reported in certain coniferous species. In loblolly pine racial tests there has been better survival during drought periods among trees from the drier, western part of the pine region than from farther east (Wakeley 1955, Zobel 1955). Meuli and Shirley (1937) found variation in drought resistance in green ash (*Fraxinus pennsylvanica* (Borkh.) Sarg.). Resistance was reported to increase geographically from south to north and from east to west in North America, and was greatest among trees grown from seed originating in regions with the longest drought period.

There is usually a wide variation within a tree species in time of leafing-out and of the onset of winter dormancy. As a general rule, it can be stated that in a given test, trees from northern localities begin leaf and shoot growth earlier in the spring than trees from southern localities. At a given locality, trees from high elevations leaf out earlier and become dormant earlier than trees from low elevations (Engler 1905, Cieslar 1907).

The time of onset of dormancy is influenced by photoperiod. Pauley and Perry (1954) for example, reported that cessation of shoot growth in *Populus* was related to day length of the seed source. Olmsted (1951), using a single seed source, found naturally decreasing photoperiod to be the primary stimulus to leaf coloration and abscission in sugar maple although growth initiation appeared to be a more complex process, strongly influenced by length of chilling period and other climatic influences.

There is some evidence of racial variation in resistance to disease. A relationship to altitude of seed source was reported at an early date in Norway spruce (Engler 1905) and has also been found in larch (Rubner 1954). Regional variation exists in Scots pine, northern races being most resistant to needle-cast disease (*Lophodermium pinastri*). Wakeley (1944, 1951) reported geographic differences in resistance to rust (*Cronartium fusiforme*) in loblolly pine.

Branch and foliage characteristics often show geographic or ecotypic variations which are related to vigor and winter hardiness, as in the case of Norway spruce (Sylvén 1909, Rubner 1941). Variation in branch and foliage characters may be of a continuous type. In Douglas-fir, for example, there is evidence of a lack of distinct separation between the coast and Rocky Mountain forms with respect to foliage and other taxonomic characteristics. Peace (1948) states that "there is a complex of variables between two extreme types" and does not favor attempts to establish numerous taxonomic subdivisions. In sugar maple clinal (continuous) variation in the shape of the leaf and character of pubescence was demonstrated by the systematic sampling study of Desmarais (1952). In white ash, the northern ecotype is distinguished by reddish petioles and leaves that are glossy above and pubescent beneath (Wright 1944).

Taxonomy and Phylogeny of Sugar Maple

Several taxonomic groupings of sugar maple are recognized, based chiefly on leaf form. These have been listed as separate species by some systematists, while others have listed them as varieties or subspecies. Sargent (1891) found gradations between them in leaf characteristics and listed them as varieties of a single species, *Acer saccharum*. Later they were grouped by Pax (1902) as separate species in the section *Saccharina*. Rehder (1940) follows this grouping and gives them full specific rank as follows:

<i>Acer saccharum</i> Marsh.	<i>Acer leucoderme</i> Small
<i>Acer nigrum</i> Michx. f.	<i>Acer grandidentatum</i> Nutt.
<i>Acer floridanum</i> Pax	

Recent studies of leaf variation in sugar maple show that there is introgression between several of these forms. On this basis they have been listed as subspecies, with *Acer saccharum* Marsh. as the type species (Anderson and Hubricht 1938, Dansereau and Lafond 1941, Dansereau and Desmarais 1947, Desmarais 1952).

Acer saccharum probably existed as a species prior to Pleistocene glacial periods (Braun 1950, Stebbins 1950). If this is true, any effect of cold period migrations on genetic differentiation has been within an already existing species. Evidence of migration in glacial and post-glacial times is very sketchy. According to one hypothesis, sugar maple moved northward with the retreat of glaciation by two routes; the first movement was northward along the Appalachians. Movement northward across Ohio and Indiana was delayed by a warm, dry post-glacial

period. According to this hypothesis, the beech-maple forests of the northern Lake States were derived from westward expansion after the northern migration and not from migrations from the south (Braun 1950). Alternatively, there may have been migration with equal rapidity to the west and north from a southern Appalachian refugium, with subsequent elimination of the *saccharum* type from the central western part of the region, leaving *nigrum*. With the return of a cooler and more humid climate, according to this view, *saccharum* is expanding its range. The *nigrum* type is apparently better adapted to dry, prairie regions, and is the only form now found in central and western Iowa (Aikman and Smelser 1938, Desmarais 1952).

The *floridanum* element is the sugar maple now found in the gulf and Atlantic coastal plains. It also extends into the Piedmont region. The ecology of *floridanum* indicates that it may be a relict from past migrations occurring in scattered localities where northern plant species persist (Braun 1950).

MATERIALS AND METHODS

The experiments were initially conducted in the greenhouse and later transferred to field plots adjacent to the Secrest Arboretum, Wooster, Ohio. The so-called "constant-environment garden" technique was used, as described by Turesson (1922) and Stebbins (1950). Seed collections were obtained from the sample localities shown in Figure 1, with particular effort to obtain the seed from representative trees native to the locality. The range of *floridanum* was included, but not that of *grandidentatum*, which extends west to Wyoming and south to Mexico. It was not possible to obtain seed of *leucoderme*, which is comparatively rare and restricted in its southern Appalachian range. In most instances a minimum of five parent trees per seed source were sampled. Each seed collection was shipped in a separate polyethylene bag with an enclosed aluminum tag, and was supplemented by a field label and a herbarium specimen of the female parent.

Seed was stratified for a period of approximately ninety days in moist sphagnum moss at 38° F., and planted in flats in the greenhouse in late January, 1954. Seed collections were randomized in the flats.

The initial period of greenhouse study of the seedlings made possible early analysis of differences, and later comparison with response in the field environment. The seedlings were transferred to the experimental nursery in the spring of 1954, where they were planted according to a statistical design. Each plot was split into two subplots, one consisting of trees from the greenhouse flats ("A" subplots), the other

consisting of seedlings grown in the nursery from seed not used in the greenhouse experiments ("B" subplots). The nursery design permitted comparisons of progeny from individual parents of the same source, as well as comparisons between sources. It also permitted omission of any number of sources in a particular comparison, in case of partial mortality.

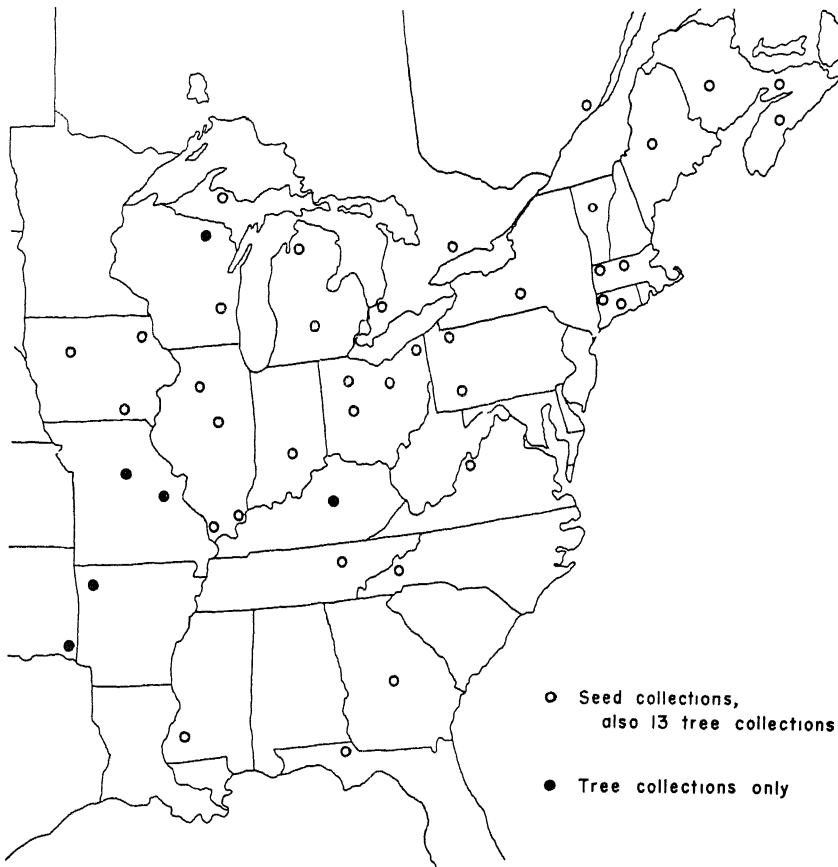


Fig. 1.—Sources of seed and trees.

A minimum of six trees per source was obtained for the supplementary field test, which included eighteen localities in the United States. The trees were mostly 3 to 4 feet in height, and were shipped bare root. They were stored over winter at 38° F. and planted in a permanent experimental plantation in April, 1954.

Table 1 lists the morphological and physiological characteristics studied during 1954 and 1955. The results of the studies are described in the following sections.

Analyses of responses were carried beyond the comparison of sources and the delineation of regional groupings. In order to better delineate ecotypes and gradients, studies were made of responses in relation to environmental factors which might have influenced the evolution of the patterns indicated.



Fig. 2.—The experimental nursery; August, 1955.

**TABLE 1.—Types of Morphological and Physiological Characteristics
Measured in 1954 and 1955**

Nature of variation and character measured	Experimental area	1954 dates	1955 dates
1. Climatic tolerance			
a. Percentage of leaf injury . . .	Greenhouse	Mar. 17	
b. Percentage of trees with fully green leaves	Nursery	Sept. 8	
c. Number of trees with some leaves turning brown .	Nursery		Aug. 12
d. Number of trees with all leaves brown	Plantation		Aug. 17
e. Number of live trees	Nursery		July 22
f. Number of inches main stem killed back	Greenhouse	May 7	
	Nursery	Sept. 7	Apr. 26, Aug. 8
	Plantation		Sept. 19
2. Growing period			
a. Stage of leafing-out	Nursery		
b. Number of trees still growing . .	Plantation	Apr. 30, May 18	Apr. 13, 18, 20, 29, May 5
c. Number of trees with winter buds	Nursery	Sept. 3	Apr. 13, 19, 29, May 5
d. Stage of fall leaf coloration	Plantation		July 13—Nov. 12*
	Plantation	Aug. 31	July 13—Nov. 12*
3. Morphology			
a. Tree form (broad, intermediate, narrow) . . .	Nursery	Oct. 11, 18, 22	Oct. 12, 18, 27
b. Leaf outline	Plantation		Oct. 8, 12, 18
c. Number of trees with forking due to stem injury . .	Nursery	Sept. 8	
d. Number of trees with forking not due to stem injury	Nursery		Aug. 8
e. Total number of trees forked . .	Plantation		Aug. 8
f. Number of forks per tree not due to stem injury . .	Nursery		Sept. 15
g. Total number of forks per tree . .	Plantation		Aug. 8
4. Other responses			
a. Total height	Greenhouse	May 7	
b. Summer leaf color	Nursery	Sept. 8	
c. Leaf damage by caterpillars . .	Nursery	Sept. 9	Oct. 5—8†
d. Leaf thickness . .	Plantation	Aug. 31	
e. Thickness of upper leaf epidermis .	Nursery		May 18, 25
f. Chromosome number	Plantation		May 26
	Nursery		Aug. 22
	Plantation		Aug. 22—23†
	Nursery		May, Aug.†

*At 4 to 5 day intervals.

†More than one day required to obtain all measurements.



Fig. 3.—The permanent plantation, including trees from eighteen sources; August, 1955.

TOLERANCE OF CLIMATIC EXTREMES

Capacity to Endure Summer Heat and Drought

The wide range of sugar maple includes regions with high summer temperatures and low rainfall. In these regions the species is restricted to comparatively cool, moist microclimates (Aikman and Smelser 1938), indicating that summer temperature and moisture conditions are critical factors limiting the species distribution. The results of the present studies demonstrate that there is geographic differentiation within the species, in both resistance to leaf desiccation from high insolation (sunsorch) and capacity to survive under drought conditions.

RESISTANCE TO SUNSCORCH

Injury to the leaves of the seedlings was a very common condition during the early months in the greenhouse, and again to a lesser extent in the nursery during both summers. It was characterized by browning from the edges inward, with gradual necrosis and eventual dropping of the leaf. There was a very noticeable variation between seed sources. This leaf injury could not be attributed to an insect or fungus disease, and was only found on trees exposed to high temperature and full solar radiation. Sunscorch is a common condition in thin-leaved trees like maple, and is associated with conditions of drought and high temperature (Baxter 1952).

Analysis of leaf injury was made on three occasions: once in the greenhouse in March, 1954, once in the nursery in early September, 1954, and again in the nursery in August, 1955. In all three investigations, leaf injury was found to be closely correlated with average July temperature of the seed source. Correlation analyses also were made using maximum summer temperature (highest ever recorded). Correlation of leaf injury with maximum summer temperature was high in

TABLE 2.—Relationship of leaf injury from sunscorch to summer temperature conditions of the source locality

Factor measured	Percent of leaf surface area injured	Percent of trees with fully-green leaves	Percent of leaf surface area injured
Location	Greenhouse	Nursery	Nursery
Date	Aug. 17, 1954	Sept. 8, 1954	Aug. 12, 1955
Coefficient of correlation with average July temperature	— .647***	+ .761***	— .731***
Number of sources	25	29	29
Coefficient of correlation with highest temperature ever recorded (U. S. sources only)	— .649***	+ .292	— .450*
Number of sources	23	27	25

*Significant at the 5 percent level.

**Significant at the 1 percent level.

***Significant at the 0.1 percent level.

the greenhouse, but not very significant in the nursery tests. The results of these simple correlation analyses are given in Table 2. A representative relationship is shown graphically in Figure 4. Extreme maximum temperature data were not available for Canadian sources; hence these were excluded from the maximum temperature correlations.

The results of the three studies of variation in leaf injury are combined in the values shown in their geographical positions in Figure 5. There are zones of relatively abrupt transition; these are roughly indicated by broken lines.

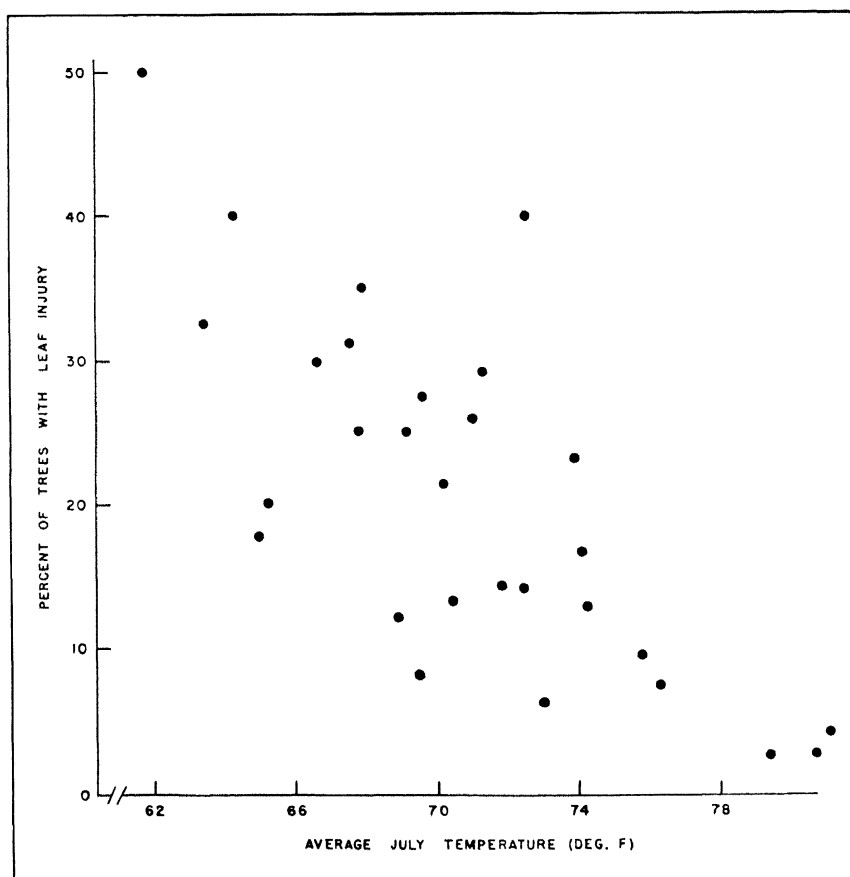


Fig. 4.—Scatter diagram of the relationship between the extent of leaf injury from sunscorch and the average July temperature of the seed source. (Nursery, August, 1955.)

The most severe leaf injury was found in trees from the region including the Appalachians, the Northeast, the northern portions of the Lake States, and adjacent parts of Canada. This is the region which has been termed by ecologists the “northern hardwood” region; Nichols (1935) calls it the “hemlock-white pine-northern hardwood” region.

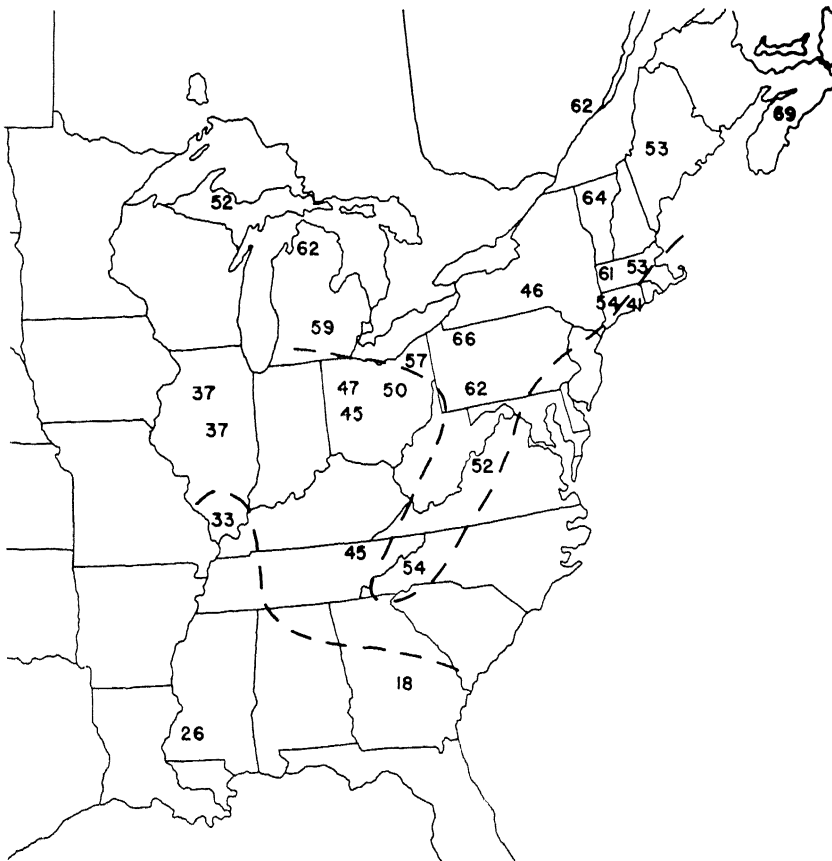


Fig. 5.—Mean percentage of leaf injury from sunscorch, with approximate ecotype boundaries. (Nursery trees).

The pattern of variation in average July temperature of the sources is shown in Figure 6, with the 75° and 80° isothermal lines (U. S. Dept. Agr. 1941) superimposed. As would be expected with highly significant temperature correlations, there is a resemblance between the pattern of variation in leaf injury and the summer temperature pattern for the sources; there is also a noticeable similarity between the zones of sharp transition and the isothermal lines.

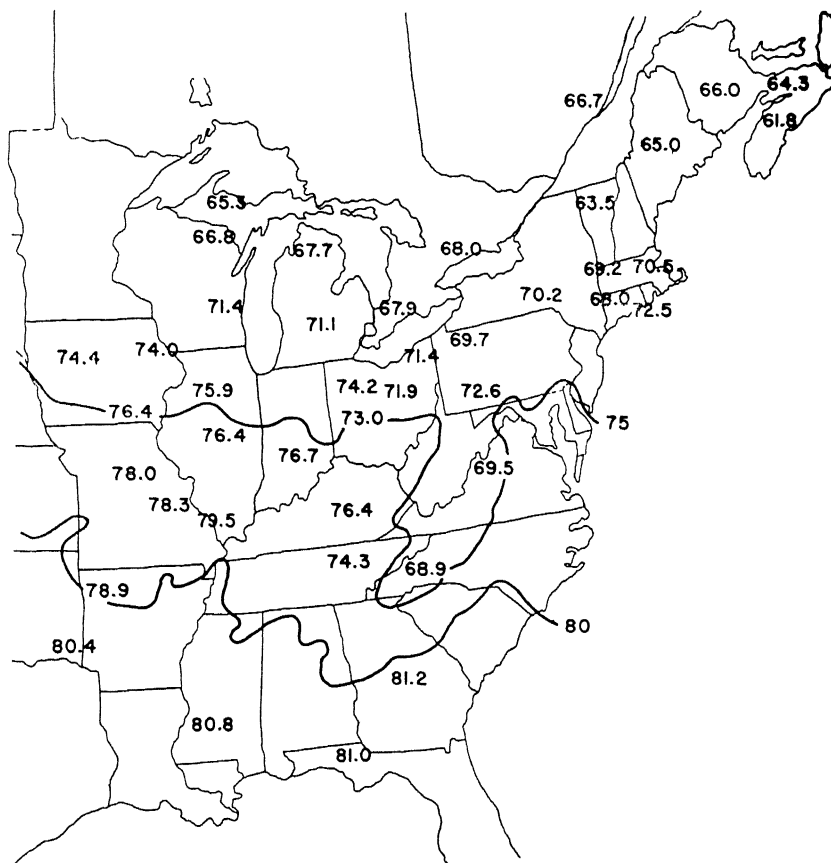


Fig. 6.—Average July temperature of each source of seed and seedlings and 75° and 80° isothermal lines of average July temperature; data from U. S. and Canadian Government weather records.

The region including trees with a low percentage of summer leaf injury is approximately the same as the range of *floridanum* as outlined by Desmarais (1952). Nursery trees from this region have the small leaves characteristic of *floridanum*. The region includes the Gulf Coastal Plain sources and extends up the Mississippi valley into southern Illinois. The response pattern, as roughly indicated, bears some resemblance to warmer temperature isotherms, in the range of 80°. There is more similarity of response between widely separated sources of *floridanum* than between *floridanum* and most of the adjacent sources.

Within the remaining part of the species range there is some variation, but no abrupt transition. There is evidence of an east-west cline in the middle latitudes, ranging from moderately high injury in Ohio to moderately low injury in Illinois.

There are statistically significant differences between the means for the regions as outlined in Figure 3. However, less importance should be attached to these differences than to the correlations, because of the fact that grouping is to some extent an arbitrary process, and there are probably a number of slight variations in grouping which would give significant results. The demonstrated relationship to summer temperature is the most reliable basis for the approximate divisions presented.

The total picture of variation in leaf injury indicates that there are three broad ecotypes, one corresponding with the northern hardwood region, another coincident with the range of *floridanum*, and a third including the remaining portion of the range of *Acer saccharum*. The ecological significance of these groupings is suggested by the correlation of variation in this response with the geographical pattern of average July temperature.

The unknown effect of other ecological factors and the lack of detailed representation from some areas prevent more precise delineation of the groupings. Actually, precise delineation of such regional patterns is impossible in any case, because of the irregularity of local conditions, just as the precise delineation of a particular temperature pattern is impossible, because of the irregularities associated with microclimate.

Studies of leaf anatomy did not yield any results which might offer an explanation of variation in resistance to desiccation. Neither leaf thickness nor thickness of the upper epidermal cells varied according to the provenance, although there was considerable random variation. If there are differences, they are extremely small and would require analysis of large numbers of leaves for detection. Possibly another type

of modification, such as the number of conducting tubes per unit of leaf surface area, would have shown a relationship to relative resistance to leaf injury.

DROUGHT RESISTANCE

Severe drought conditions prevailed during the 1954 growing season at Wooster. Table 3 includes pertinent data, taken from the Monthly Weather Report of the Ohio Agricultural Experiment Station.

TABLE 3.—Monthly precipitation records for the 1954 growing season at the Ohio Agricultural Experiment Station, compared with the long-term averages for the same weather station

Month	1954 precipitation inches	67-year average precipitation
April	5.30	3.10
May	1.17	3.81
June	1.74	4.00
July	1.57	3.89
August	2.40	3.50
September	1.88	3.04
October	7.04	2.44

The drought caused very high losses in the nursery. Survival counts showed mortality was not a sudden process. There were high losses both before and after the tally taken on September 7, 1954, as shown by later survival data. At the end of the first growing season, about 2,000 of the original 9,229 seedlings were living. In spite of this high rate of loss, there were still sufficient numbers of trees from nearly all provenances for statistical comparisons and for later transplanting to permanent experimental plantations.

An analysis of the 1954 nursery data did not show significant differences in survival between seed sources, nor between replications. The difference in survival rate between trees grown in flats and the smaller trees started later was highly significant; the larger, older seedlings had a much higher percentage of survival. This difference was constant for all seed sources; it did not depend on the origin of the seed.

Other variance analyses of the 1954 data were made for the older and younger seedlings independently. The smaller trees, taken alone, showed significant differences in survival between different parts of the

nursery, and to a lesser extent between sources. Later analysis was restricted to the trees in the "A" subplots, because of the high losses in the small trees and their great variation in survival between replications. The 1955 measurements did not bring out any significant differences between provenances in survival percent.

There were significant correlations between survival rate and summer temperature conditions of the provenance, although the correlations were not as high as they were for leaf injury. Survival rate

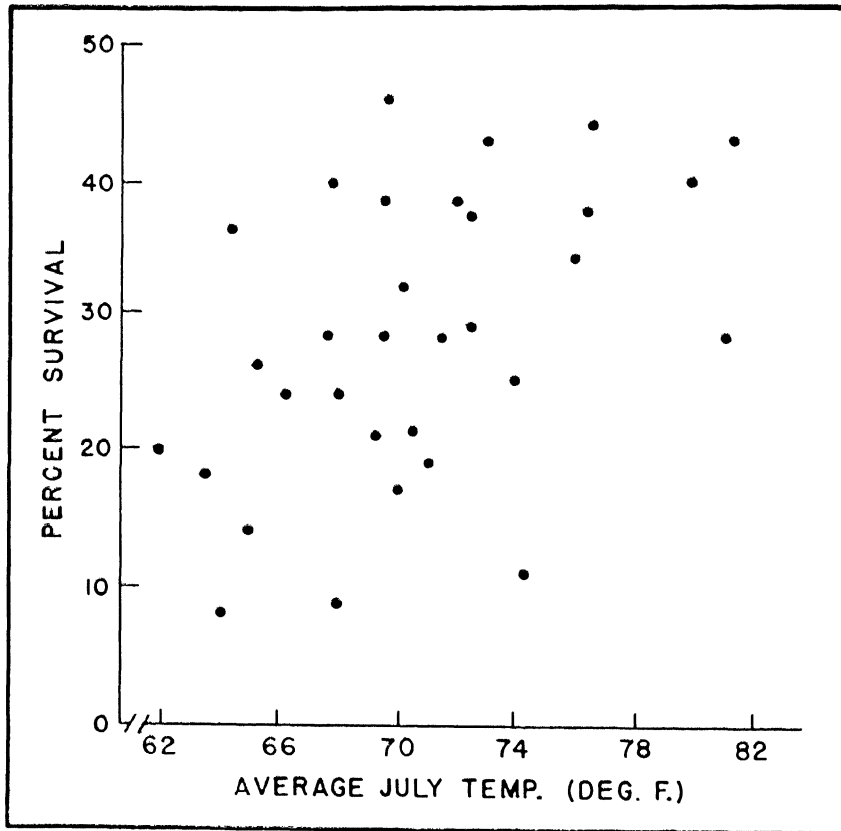


Fig. 7.—Percentage of survival after drought in relation to average July temperature of the seed source. (Nursery trees.)

was more dependent on extreme maximum temperature of the source than on average July temperature. The relationships found by correlation of survival percent with average July temperature and maximum summer temperature are shown in Figures 7 and 8.

The results of the correlations provide statistical support for the groupings indicated in Figure 9. When the responses are plotted geographically, differences are noticeable between trees from the "northern hardwood" region on the one hand and trees from the central and southern states on the other. There are irregularities in the

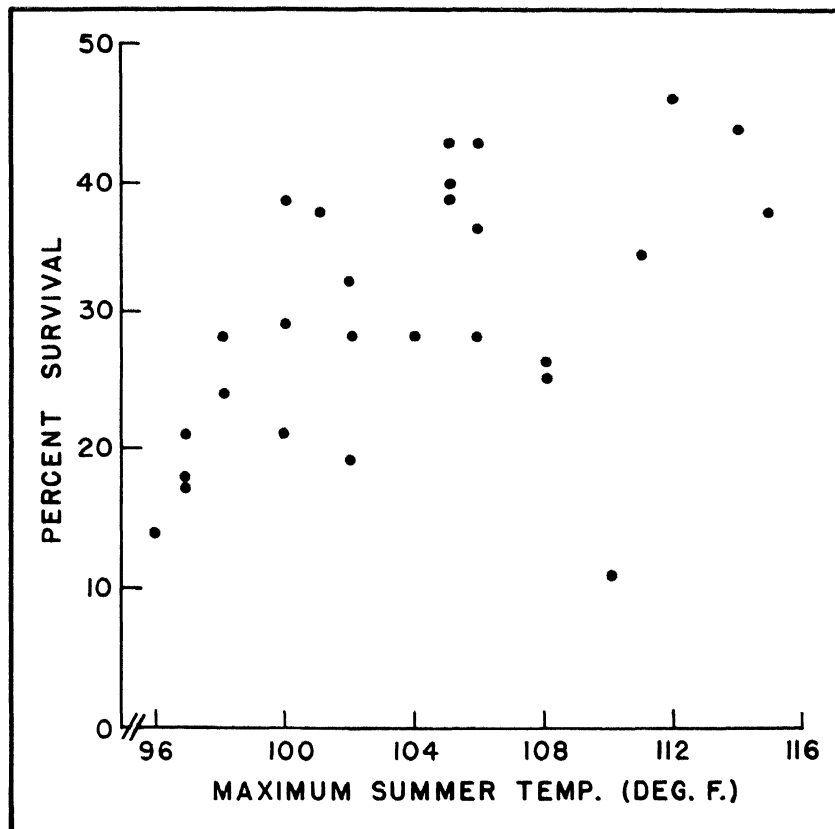


Fig. 8.—Percentage of survival after drought, in relation to highest temperature ever recorded for the seed source. (Nursery trees).

pattern, but the overall geographical distribution of the responses indicates the same arrangement of ecotypes as did the studies of leaf scorch. Figure 9 shows comparative survival in the nursery of trees of two different ecotypes. The only apparent difference is the absence of a distinct *floridanum* grouping. Evidently trees growing in the cool, damp climate of northern and Appalachian forests produce progeny more susceptible to drought conditions than trees from the hot, dry climate of the midwest. Table 4 shows the survival rates by regions, for the "A" subplots. The difference in response between the two ecotypes is highly significant.

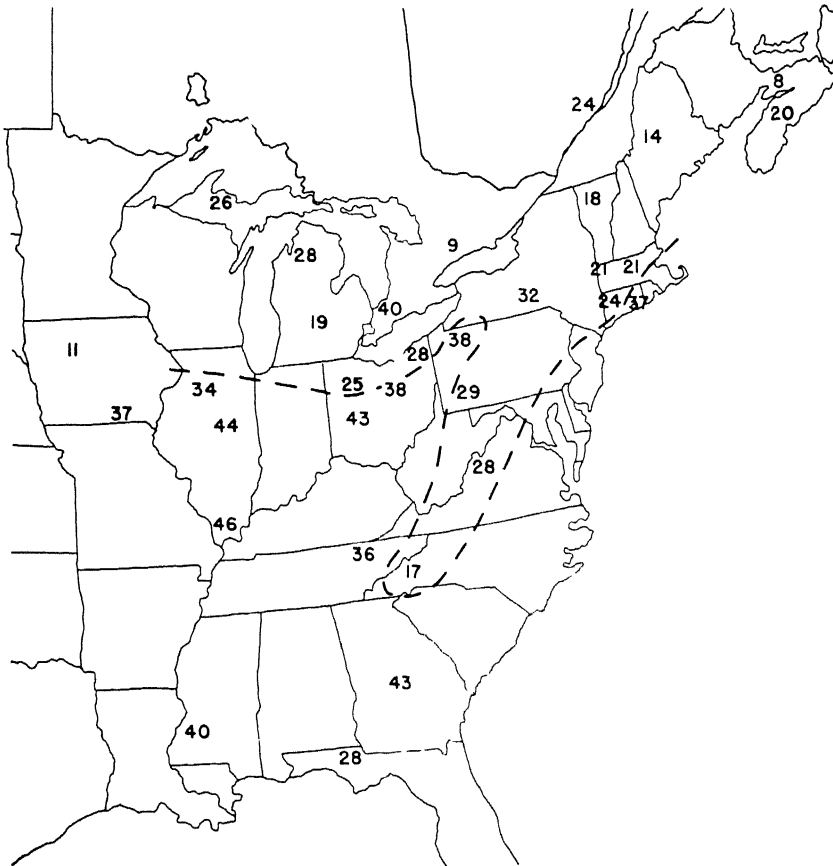


Fig. 9.—Percentage of survival after drought, with approximate ecotype boundaries. (Nursery trees).

TABLE 4.—Number of nursery trees from two regions surviving summer drought conditions. Data of April 26, 1955, "A" subplots

	Alive	Dead	Total
Northern	579	1982	2561
Central-southern	551	864	1415
Chi square = 119.52***			

In the plantation, Appalachian trees were the only ones with a high mortality rate. Almost all Virginia trees died during the first growing season. These losses were replaced, but most of the replacements died in 1955. The loss rate was also high among trees from North Carolina and Pennsylvania.

The physiological basis of this regional variation in drought resistance has not yet been investigated. A comparative study of root systems of the two ecotypes will be made at the time of transplanting. It is quite possible that a more pronounced tap root may be present in southern trees, as Wright (1944) found in white ash, although Wright did not report differences in drought resistance.

INFERENCES CONCERNING DROUGHT RESISTANCE

The inferences drawn from these studies of variation in drought resistance are:

1. Environmental conditions to which the seedlings were subjected had a strong influence on the rate of survival in the nursery. These environmental conditions may include such influences as small site differences within the nursery and variations in weather conditions during the planting period. Among the large trees in the plantation, environment was not so important.

2. There are, nevertheless, differences in capacity to survive summer drought conditions; these differences depend upon the origin of the seed. The highest drought resistance is found in trees from hot, dry climates and the lowest resistance in trees from cool, moist climates.

3. The geographical pattern in the northern and central regions conforms with that found in studies of comparative leaf injury, although it cannot be as sharply defined as the latter. There are irregularities in the pattern, and there is great variation in response between individual trees.

4. High air temperatures during the growing season have played some part in the evolution of drought-resistant genotypes of sugar maple. However, survival is probably more closely related to soil moisture conditions than to air temperature. Trees from dry regions may be better adapted to dry soils than trees from humid regions.

A few other studies were made of types of plant injury or mortality in relation to ecological factors. No trends were found. The following analyses were made: (1) percentage of leaf injury in relation to average June-to-August precipitation of the seed source (data of March, 1954 and September, 1954); (2) percentage of survival in relation to average June-to-August precipitation of the seed source (data of September 1954); (3) percentage of damping-off in relation to (a) maximum summer temperature, (b) average July temperature, (c) minimum winter temperature (data of February, 1954).



Fig. 10.—An example of the maximum extent of regional variation in survival after a drought period, showing a high survival rate among trees from central Illinois (left foreground), and almost total mortality among trees from the Southern Appalachian highlands (right foreground).

Winter Hardiness

In the current studies, there was very little mortality among the nursery seedlings during their first winter (1954-55), and there were no winter losses in the plantation.

The May 5, 1955 survey showed that killing-back of shoots of *floridanum* trees for a few inches was a common condition, but that hardly any trees from other regions were affected. The effects on these southern trees are shown in Table 5 ("A" subplots only).

Frost injury was observed during November, 1954 and again in November, 1955, although it was not as severe as expected. The lath screens, which were kept over the beds during the first winter, probably reduced the damage during the late fall of 1954, although damage during the following fall was not severe. In both seasons, many trees from these southern sources were still growing after several frosts. In 1954, some *floridanum* trees were still growing on November 17, after a total of 23 days with minimum temperatures of 32° F. or below (according to Experiment Station weather records). The minimum temperature for the first winter at the weather station was -5° F., on January 31, 1955, and there were three periods during which the temperature fell below zero.

TABLE 5.—The effect of frosts on *floridanum* seedlings in relation to winter conditions of the seed source. Nursery, "A" subplots, data of May 5, 1955

	Seed Source		
	Franklin Co., Mississippi	Bibb Co., Georgia	Jackson Co., Florida
Percentage of trees affected	43	54	83
Average number centimeters main stem killed back	5.1	5.1	5.8
Average January temperature of seed source (Deg. F.)	51°	47°	53°
Lowest temperature ever recorded for seed source (Deg. F.)	8°	-4°	13°

Late spring frosts in 1955 caused shoot injury to nursery trees from the most northern provenances, but had much less effect on the southern trees. These frosts occurred on May 9 and May 18, after the survey of winter injury had been made. The effects were recorded on August 8, 1955 in a study of forking. The Canadian and northern Michigan trees were the first to break dormancy in the spring (Fig. 14), and by the middle of May were in full leaf and in the stage of stem elongation. Trees from New England and central latitudes were growing, but were not as far advanced with respect to stem elongation. Similar effects were noticed (but not systematically recorded) in the plantation.

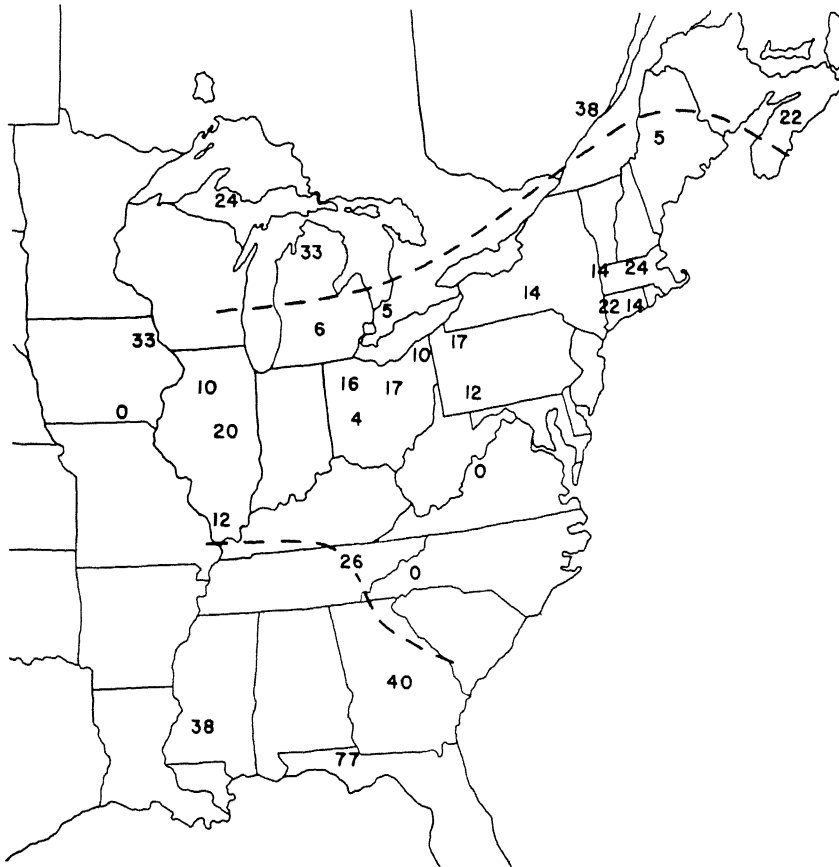


Fig. 11.—Percentage of trees with forking resulting from frost injury to shoots, with approximate regional groupings. (Nursery, 1955.)

Figure 11 illustrates the relationship of cold injury to provenance. Trees from central latitudes had the least forking caused by frost damage. Within this region there is considerable variation in the length of the growing season, but the trees are neither extremely early in initiating growth in the spring nor do they continue growing late into the fall. They are, therefore, less subject to fall frosts than are southern trees, and less subject to spring frosts than are northern trees. These regional differences are statistically significant (Table 6).

TABLE 6.—Regional comparisons of numbers of trees with forking caused by frost injury to shoots. Nursery, "A" subplots, 1955

Region	Forking from Frost Damage	
	Present	Absent
Northern	34	79
Central	86	514
Southern (<i>floridanum</i>)	49	67

Statistical comparisons:

Northern versus Central Chi square = 18.27***

Central versus Southern Chi square = 42.26***

TIME OF GROWTH INITIATION AND CESSATION

Time of Growth Initiation

The time of flushing in sugar maple was found to be under rather rigid genetic control. There was only minor variation in response between trees from the same source. This was true even in the plantation, with only six trees representing each provenance.

A simple scale was devised to measure the stage of bud-breaking and leaf development. This was found to be workable in the plantation and nursery in 1955. The nursery could not be analyzed for growth initiation in 1954, because of the preliminary period of growth in the greenhouse.

There were highly significant differences between provenances in the time of flushing in the plantation. Measurements made on April 30, 1954 showed large differences between sources; by May 18 the late-flushing sources were overtaking the others and differentiation was less apparent. In 1955, flushing started earlier; April 13 measurements are comparable with those of April 30, 1954.

A test of "least significant difference" was made of the April 30, 1954 data, after the sources were ranked in order of magnitude of response. There was no significant difference between sources adjacent in the ranking, in spite of the results of the analysis of variance, although there were significant differences between non-adjacent sources (Table 7). A north-to-south trend is apparent in the ranking. In this case, variation clearly exists but is of a continuous nature, resulting in a graded series of small differences, none of which are large enough to be significant in a ranking test.

The results from the 1955 nursery data are very similar to those obtained from the plantation. Differences between seed sources in time of leafing-out were highly significant, while location in the nursery had no effect. Analysis of the split plots showed that the larger trees started in flats leafed out earlier than the smaller trees which were started later.

A gap test was applied to the ranked values. As in the plantation, there was a graded series of small differences, with no pronounced gaps.

TABLE 7.—Stage of leafing-out in the plantation on April 30, 1954

Source	Total Index Value	
N. Wisconsin	29	
N. Michigan	29	
New York	27	Least significant
S. Michigan	27	range (between non-
Ohio	22	adjacent values)=15
N. W. Massachusetts	21	
Cent. Massachusetts	21	
Pennsylvania	21	Least significant
S. Wisconsin	16	difference (between
Illinois	16	adjacent values)=6
Tennessee	15	
Kentucky	14	
Arkansas	14	
Missouri	9	
Virginia	8	
North Carolina	6	
Oklahoma	6	
Georgia	6	

ANALYSIS OF LEAFING-OUT IN RELATION TO EVOLUTIONARY INFLUENCES

The apparent clinal trend was examined in greater detail, using nursery data and restricting analysis to the "A" subplots. This made it possible to include more seed sources and thereby obtain a more precise variation pattern. Studies were made of the relationship between the time of flushing and certain basic environmental factors; namely, photoperiod (day length) and temperature. These are factors of possible significance in the evolution of genotypes adapted to particular parts of the species range. Continuous geographic variation, if it actually exists, presumably resulted from the action of one or more environmental influences which in themselves have this type of variation. Latitude was used as a measure of the photoperiodic effect.² Temperature was measured in two ways: (1) average July temperature, to evaluate the relationship of prevailing warm season temperature to growth initiation; (2) average length of frost-free period (growing season), to evaluate the possible selective action of early and late frosts on genetic differentiation.

There are high correlations among the environmental factors themselves. Consequently, simple correlation with each of these variables separately could give misleading results. In order to test independent relationships, the technique of partial or multiple regression was applied, to assess the relative importance of latitude, temperature, and length of growing season.

Records of average length of frost-free period are not listed in Canadian meteorological summaries (Canadian Dept. of Transp. c. 1947). Therefore this analysis was limited to trees from sources within the United States.

The results of the four-variable partial regression analysis are given in Table 8. There is a highly significant relationship between time of leafing-out and the combined effect of seed source conditions of summer temperature, photoperiod, and length of frost-free period. Much of this "combined" effect cannot be divided into individual effects, because of the close interrelationships.

²The relationship of latitude to day length is approximately linear during the summer months, within the range of latitudes included in this experiment (Marvin 1905). Latitude was used as a measure of photoperiod by Pauley and Perry (1954) in studies of variation in **Populus**.

TABLE 8.—Partial regression of time of flushing on average July temperature, latitude, and average length of growing season of the seed source; mean squares and significance levels obtained in three separate analyses. Combined nursery data from four dates in April, 1955

Effect on the regression	Four Variables	Three Variables	
	"A" subplots, 4 blocks, 23 sources	"A" subplots, 4 blocks, 27 sources	All "A" trees, 32 sources
Combined effect of measured environmental influences	29.35***	62.17***	54.95***
Independent effect of temperature	6.30	7.54	5.35
Independent effect of latitude	10.07	18.86**	17.39*
Independent effect of length of growing season	.29	—	—
Residual variation (error)	2.71	2.41	2.71

The analysis indicates that both average July temperature and latitude taken individually bear some relationship to time of leafing-out, but that neither stands out as the predominant influence. Length of growing season shows no correlation with time of leafing-out, when the effects of the other two factors are eliminated.

More inclusive evaluation is possible if only latitude and average July temperature are included in analysis. Length of growing season is omitted because it does not contribute materially to the total regression. Canadian sources can then be included. Using this procedure, results of two separate partial regression analyses again show that the combined temperature-latitude relationship is highly significant (Table 8). They also bring out more strongly the closer relationship to latitude than to temperature. Since latitude (or photoperiod) is a continuous variable, it could be partly responsible for apparent clinal variation in time of growth initiation.

The relationships are shown graphically in the scatter diagrams of the data from one of these analyses. The graphs show the distributions which would be obtained from two simple regressions, one on temperature, the other on latitude (Figures 12 and 13). Vertical dispersion of the responses is not as great in Figure 13 as in Figure 12. The scatter diagrams give an effective demonstration of the erroneous conclusions

that might be drawn from a simple regression. There are very definite trends in both of the diagrams; however, nearly all of the trend in the temperature diagram could be the result of its high correlation with latitude, or *vice versa*.

Table 8 is not interpreted as showing that warm-season temperature has no effect on time of flushing in sugar maple. There may be some temperature effect; the independent effect of temperature is close to the 95 percent probability level in the 27-source analysis. The temperature effect might be greater if the temperature value for each source were not a little less precise than the latitude value.

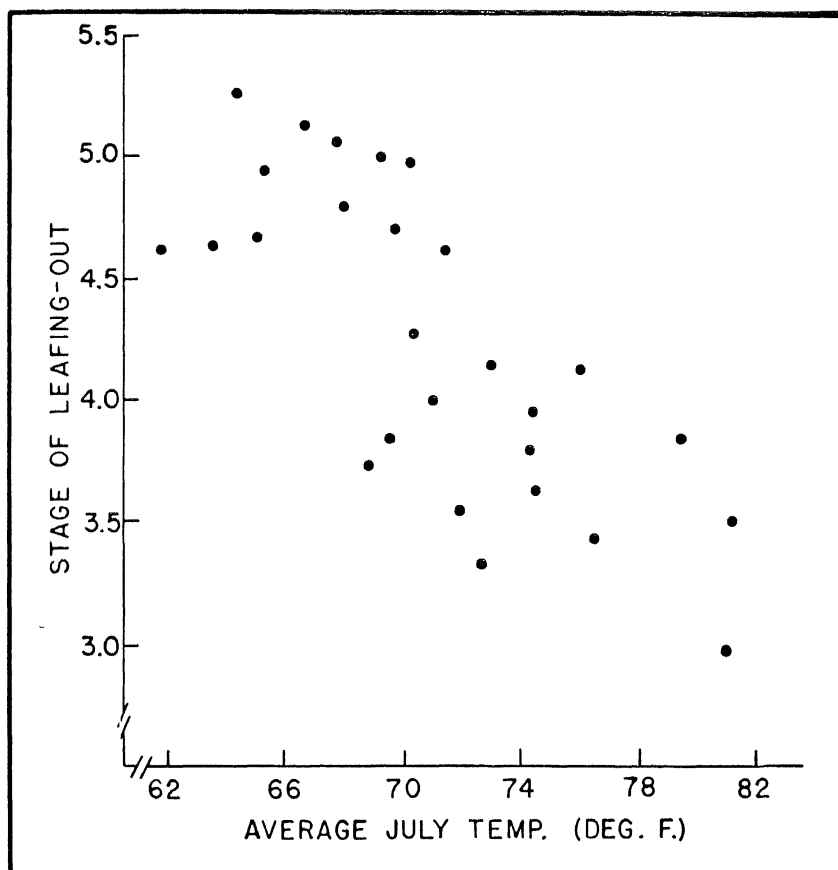


Fig. 12.—Time of leafing-out in the nursery in relation to average July temperature of the seed source.

Actually, there is evidence that neither of these environmental variables is the determining factor in leafing-out. This evidence was obtained from a study of geographic trends over the range of the species, using the following procedure: (1) scores were plotted on a series of maps, one for each of three field evaluations made in the plantation in 1954, one for each of four 1955 plantation evaluations, and one for the total nursery values for 1955; (2) approximate isometric lines (lines of equal index value) were sketched in by interpolation between points,

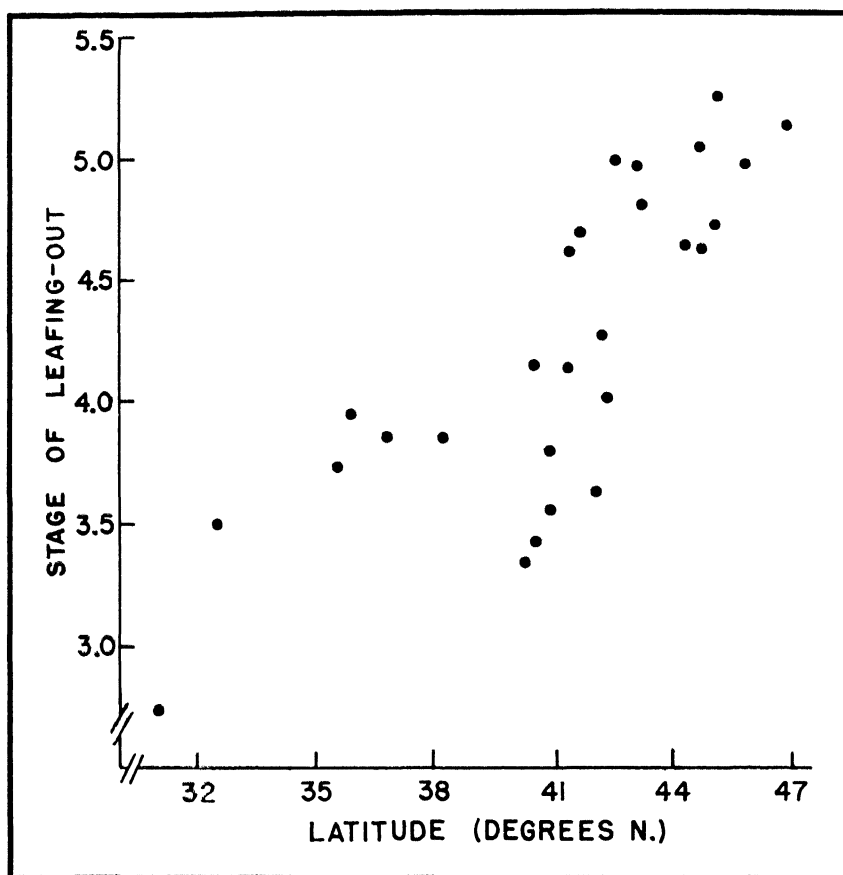


Fig. 13.—Time of leafing-out in the nursery in relation to latitude of the seed source.

using the cardinal numbers, e.g., 5, 6, 7; (3) the maps were then superimposed and the composite pattern of lines was traced on another map (Figure 14). These lines do not represent differentiation in response; they indicate relative rate of progression of flushing in population samples from different areas. They may be likened to contour lines on a topographic map, with stage of flushing instead of altitude as the variate.

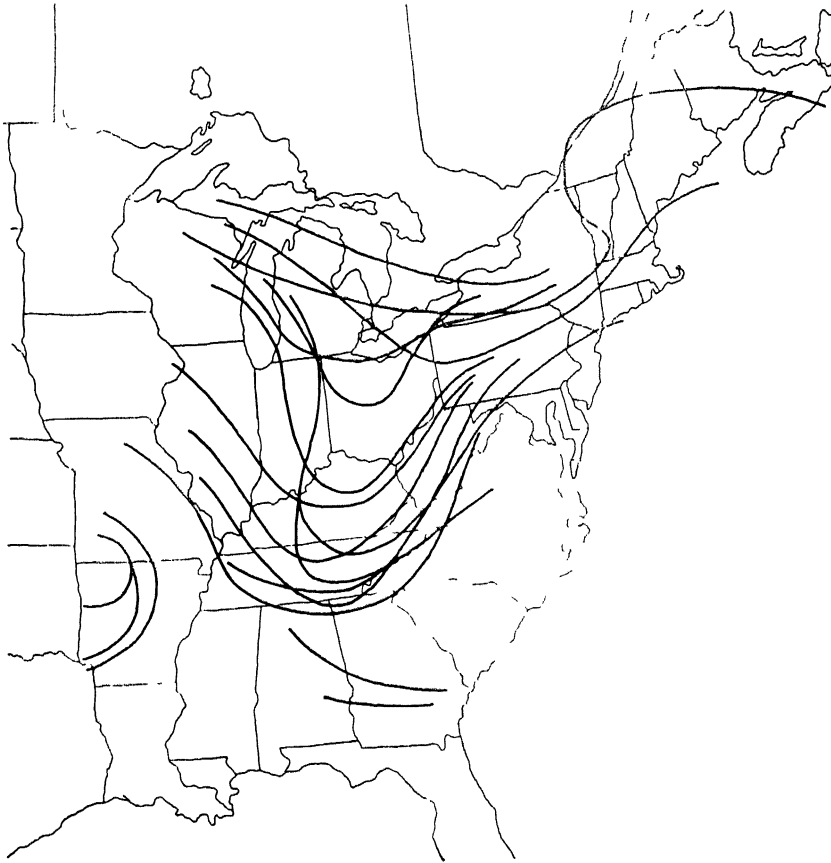


Fig. 14.—Configurations of the north-to-south cline in time of flushing in the nursery.

The superimposed lines fit together into characteristic trends, which are sufficiently uniform to demonstrate that both temperature and photoperiod could be associated with the response. It is important to remember that the trend shown is not the trend of trees in their native localities; it is the responses at Wooster, Ohio.

Temperature is not the dominant influence. If it were, the southward bulge would extend down the Appalachians, which is not the case. Flushing begins in northeastern Canadian sources, and proceeds toward the southwest provenances, pushing "down" through trees from the Ohio River Valley before reaching those from the southern Appalachians. Trees from Kentucky and Tennessee flush well ahead of trees from the highlands of Virginia and North Carolina, and growth does not begin in Illinois plots until it also begins in Tennessee plots. The flushing date of Missouri trees is approximately the same as that of Georgia trees. The Ozark-Ouachita region begins somewhat earlier than the surrounding region.

Day length does not fit the pattern very closely either, although it can be seen how it might in some regions be more closely associated with flushing than is temperature. This is certainly true in trees from North Carolina and Tennessee, where temperature differences are great but latitude is constant; the same situation is found in northern Ohio versus northern Pennsylvania.

It seems probable that there is some other evolutionary influence which has contributed to the molding of this pattern of trends. Glacial migrations might provide an explanation of the "bulge" into Kentucky and Tennessee. During Illinoian and Wisconsin glaciation, ice masses pushed southward through Ohio. Northern genotypes of sugar maple may have been gradually forced southward. By the process of natural selection, these types could have become the dominant ones in areas formerly occupied by southern or mid-latitude genotypes. A southward movement of northern races would also offer some explanation of the comparatively slight regional variation in winter-hardiness. In the Ozark region, an early-flushing response may be the inheritance from a Pleistocene migration from the north, followed by isolation during a subsequent warm period.

Time of Onset of Dormancy

CESSATION OF SHOOT GROWTH

Trees from different provenances varied in the time at which they stopped height growth and developed winter buds. In general, the trees from northern sources were the first to become dormant. The trees from far to the south continued growth until growing tips were killed by heavy frosts.

Only one survey was made in the nursery in 1954, on September 3. An estimated percentage of trees still growing was recorded for each subplot. The method was not sufficiently precise to distinguish any differences other than that between *floridanum* trees and trees from other areas.

The refined techniques and periodic remeasurement employed in 1955 made possible a more precise analysis of variation in time of height growth cessation. This analysis showed that differences between sources, although significant, were not as pronounced as one might expect. The subplot pretreatment had no effect on onset of dormancy, as it did on time of leafing-out; trees in the "A" subplots stopped growing at the same time as did the smaller trees. A significance test was considered unnecessary in the plantation, because phenological differences were large and consistent between trees from the far north and trees from the far south.

The relationship of growth cessation to ecological factors was analyzed by partial regression (Table 9). One analysis included responses of trees from 26 United States sources. As in the case of studies of leafing-out, it was necessary to omit Canadian trees in order to include length of growing season of the seed source in the analysis. Another analysis omitted length of growing season and included Canadian trees.

The results show a significant relationship between time of cessation of height growth and the combined variation of average July temperature, latitude, and length of growing season. There is some independent effect of each of these influences, in no case very great.

TABLE 9.—Partial regression of time of height growth cessation on average July temperature, latitude, and length of growing season of the seed source; mean squares and significance levels for two separate analyses. Combined nursery data for 11 dates during July and August, 1955

Effect on the regression	Four variables, Blocks I to V, 26 sources	Three variables, Blocks I to V, 30 sources
Combined effect of measured environmental influences	18.34**	29.29***
Independent effect of temperature	1.22	2.96
Independent effect of latitude	1.98	8.63
Independent effect of length of growing season	1.07	—
Residual variation (error)	3.10	2.94

The scatter diagrams (Figures 15 and 16) show the simple linear relationships of time of growth cessation to summer temperature and to photoperiod. With the exception of one point (North Carolina, Buncombe) the growth trend on latitude is fairly regular. The response is a little more irregular when related to temperature.

Neither the nursery measurements nor the plantation measurements had a recognizable geographical pattern which could be delineated on a species range map.

AUTUMN LEAF COLORATION

Leaf coloration measurements were taken in the plantation on three dates in 1954, and on three dates in 1955. Measurements were taken in the nursery on three dates in 1955. Too few sources were represented in the plantation for accurate analysis by partial regression, although casual inspection strongly suggested a north-to-south trend. The results obtained from analyses of nursery measurements are shown in Table 10. There is a very high correlation between the time of fall leaf coloration at Wooster and day length of the seed source. Neither

summer temperature of the seed source nor length of growing season seems to have any significant relationship to the time of fall coloration at Wooster. The relationships are illustrated graphically in Figures 17 and 18.

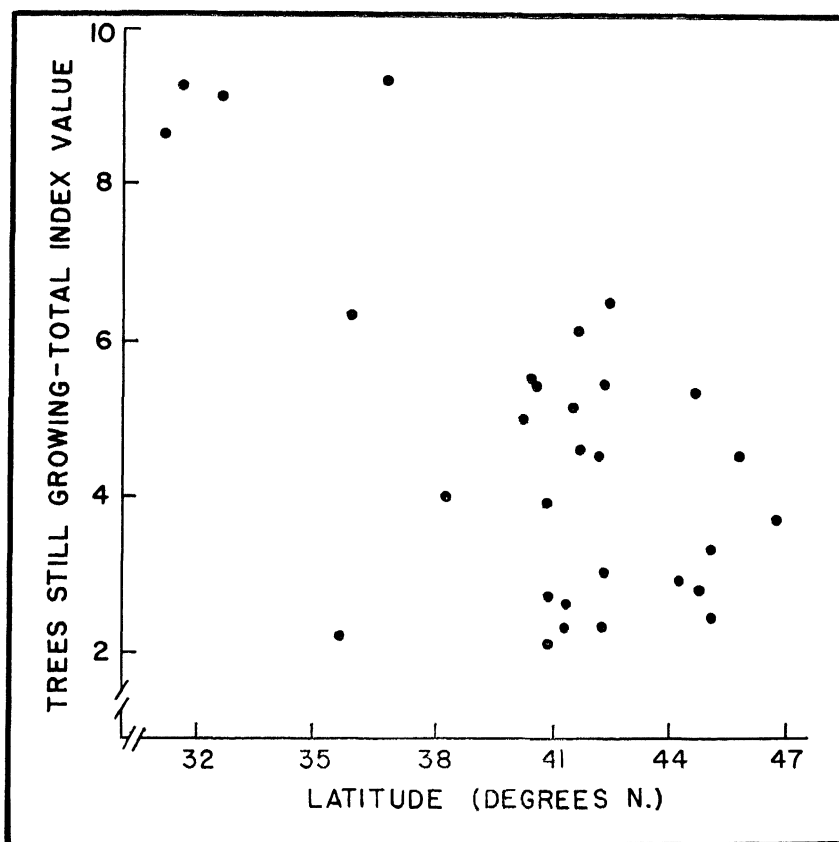


Fig. 15.—Time of height growth cessation in relation to average July temperature of the seed source. (Nursery trees.)

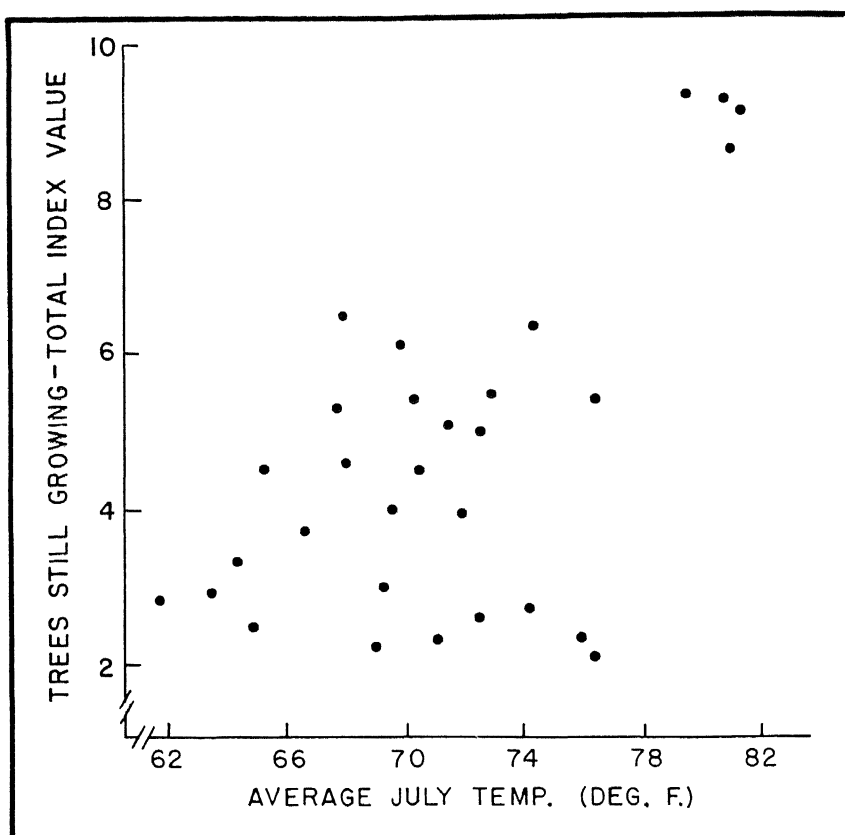


Fig. 16.—Time of height growth cessation in relation to latitude of the seed source. (Nursery trees.)

TABLE 10.—Partial regression of stage of fall coloration on average July temperature, latitude, and length of growing season of the seed source; mean squares and significance levels. Combined nursery data for 3 dates in October, 1955

Effect on the regression	Four variables, Full Plots, Blocks I to V, 22 sources	Three variables, Full Plots, Blocks I to V, 25 sources
Combined effect of measured environmental influences	6.03***	11.92***
Independent effect of temperature	.68	.09
Independent effect of latitude	4.41**	9.61***
Independent effect of length of growing season	.11	—
Residual variation (error)	.39	.38

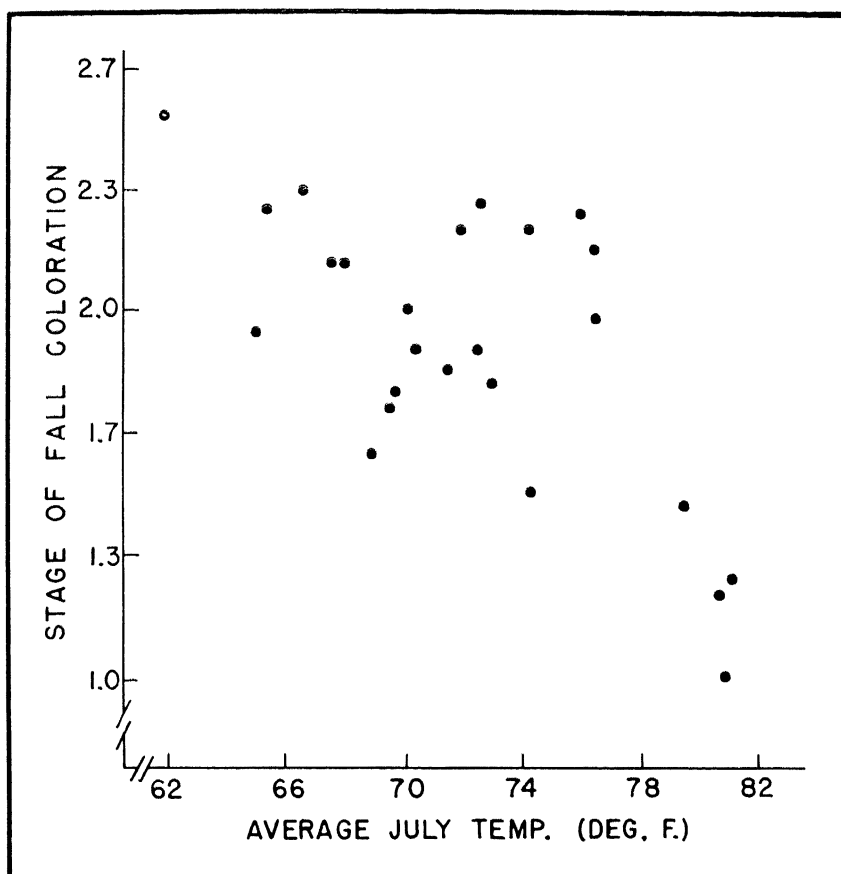


Fig. 17.—Time of fall coloration in relation to average July temperature of the seed source. (Nursery trees.)

Figure 19 shows the geographic pattern of time of leaf coloration at Wooster. Isometric lines from the three sets of data are superimposed on a single map of North America. The technique is similar to that used for the data on flushing, the lines approximating the even values or "contours" in a pattern of clinal variation. The strong latitudinal relationship is evident, in contrast to the map of trends in time of leafing-out. There is some effect of temperature, shown by the southward "dips" in the Appalachian region; these dips are similar to isothermal configurations (Figure 6), although much less pronounced. A temperature effect is also noticeable in the Ozark region, which shows an earlier fall coloration than adjacent provenances.

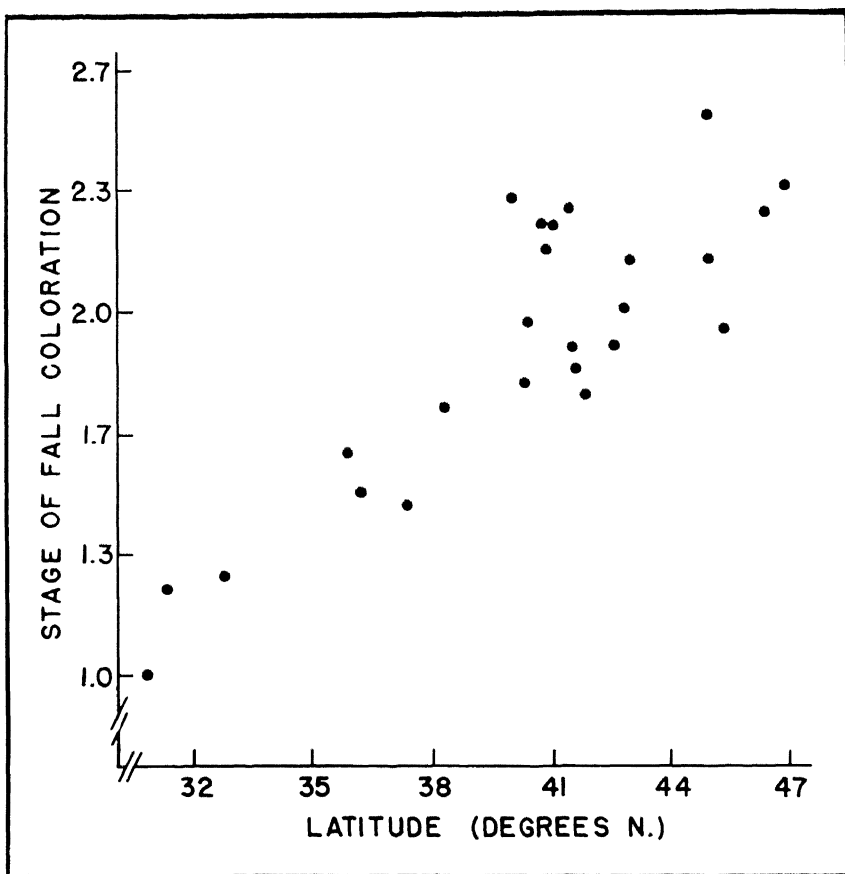


Fig. 18.—Time of fall coloration in relation to latitude of the seed source. (Nursery trees.)

INFERENCES CONCERNING VARIATION IN ONSET OF DORMANCY

The following general statements can be made from the results of the growth cessation studies. In the first place, the time of cessation of shoot growth at Wooster has some relationship to the combination of conditions of summer temperature, photoperiod, and length of growing season of the source. However, the relative importance of one of these

factors versus the other cannot be judged from the data. One problem in precise evaluation is the difficulty of accurate field measurement of the time of growth cessation, because of the lag in the development of a winter bud. Another is the unavoidable error introduced by application of climatological data to the seed source. There is no apparent geographical pattern of growth termination which can be mapped and related to any of the three ecological influences. It appears quite possible that one or more other factors are important in the process of growth cessation and bud formation.



Fig. 19.—Configurations of the north-to-south cline in time of fall coloration in the nursery.

In the second place, the time of fall leaf coloration at Wooster is much more closely related to photoperiod than to temperature, when trees from the entire species range are considered. The variation is continuous, beginning with the northern provenances and progressing through the trees in a "southward" direction, with some modifications associated with regional temperature relationships. Trees from cool temperature regions are slightly ahead of trees from warm temperature regions at the same latitude.

These results are in agreement with those obtained by Olmsted (1951) in his studies of dormancy, leaf senescence and abscission in sugar maple. From his controlled-condition experiments, using a single seed source, Olmsted concluded that the development of bud rest is a complex process, not decisively controlled by photoperiod, although this may be a contributing factor. Leaf senescence, however, as judged by loss of green color, was found to be primarily stimulated by naturally decreasing photoperiod.

PHENOLOGICAL DIFFERENCES BETWEEN BLACK AND SUGAR MAPLE

Shoot dormancy and leaf coloration developed earlier in black maple than in sugar maple. Differences were very noticeable in the plantation at the time of leaf coloration. Two of the eighteen sources represented in the plantation were black maple, including Ingham County, Michigan and Wayne County, Ohio.³

Table 11 shows the early termination of shoot growth and early leaf coloration of plantation black maples, compared with that of sugar maples with similar conditions of temperature and latitude. All six of the southern Michigan black maples stopped growing before July 13, 1955, the date when the first measurements of growth cessation were taken.

The same situation was found in the nursery, although there were some irregularities (Table 12). The measurements in the nursery were of progenies from individual female parents known to be either sugar or black maple. In some instances the progenies of black maples consisted partly or predominantly of sugar maples, presumably because of crosses with adjacent *saccharum* pollen trees. This is believed to be one reason why the contrasts in Table 12 are not as pronounced as in

³In 1955 the Ohio trees were replaced with **saccharum** for comparison with other **saccharum** trees.

TABLE 11.—Relative time of onset of dormancy among black and sugar maple trees from northern sources in the experimental plantation

Source	Total Index Value		
	Continuation of shoot growth	Progress of fall leaf coloration	
	1955	1954	1955
N. Wisconsin	1.3	7.0	9.0
N. Michigan	0.8	5.3	5.2
N. W. Massachusetts	1.0	6.6	7.0
N. Pennsylvania	1.2	6.6	—
S. New York	1.2	5.2	7.6
S. Wisconsin	2.5	5.8	5.7
Central Massachusetts	4.8	5.0	4.8
S. Michigan*	0.0	6.2	10.7
N. Ohio*	—	8.7	—
Central Illinois	3.6	5.5	5.8

**nigrum*: all others are *saccharum*.

Table 11. Table 12 differs from Table 11 by giving comparisons between black and sugar maple progenies from the same seed source, and, in the case of Ohio and Michigan trees, between trees from the same stand.

Additional observations were made on large trees in the Secret Arboretum and other locations in Wooster. Growth cessation, leaf coloration, and leaf fall took place earlier in black maple than in sugar maple. Plot D-4 of black maple in the Secret Arboretum had lost nearly all of its leaves by October 28, 1955, while most of the leaves of sugar maple in adjacent plot D-2 were still on the trees. In July, 1955 efforts to obtain developing leaves of young black maple trees for chromosome counts were unsuccessful, because terminal buds had already been formed. On the other hand, developing sugar maple leaf tissue was easy to find at this time.

These phenological differences were not apparent among the black maples from the western part of the range, including south and west-central Iowa. There are no *saccharum* progenies from these areas for comparison with *nigrum* progenies; however, the onset of dormancy was not noticeably earlier among these Iowa black maples than among trees from the nearest and most climatically-equivalent sugar maple sources, namely, progenies from northern and central Illinois collections.

TABLE 12.—Relative time of onset of dormancy in different progenies of black and sugar maple trees from three sources

Source	Female parent tree number	Total Index Value of Progeny	
		Continuation of shoot growth 1955	Progress of fall leaf coloration 1955
Michigan, Ingham County	70-71*	0.0†	8†
	73*	1.6‡	11‡
	74	0.2	6
Ohio, Logan County	127	6.0	4
	128	3.2	7
	129*	3.5‡	7‡
	130	3.5	4
	131	3.1	7
Virginia, Highland County	193*	1.5§	8§
	194	1.0	7
	195	2.0	4
	196	4.2	4

**nigrum*: others and their progenies are all *saccharum*.

†Progeny predominantly *nigrum*.

‡Progeny predominantly *saccharum*.

§Progeny equally distributed between *nigrum* and *saccharum*, with intermediates.

PHYSICAL CHARACTERISTICS

Tree Form

One type of variation in tree form has already been described. This is a tendency to fork one or more times as a result of frost injury, which in turn is the result of lack of adjustment to the Wooster growing season. The response is characteristic of trees brought too far north or too far south and would not be found in the native habitat. Therefore, it actually represents physiological variation in time of growth initiation and growth cessation, rather than an inherited lack of apical dominance.

The results of measurements of "Type B" forking (forking that could not be attributed to shoot injury) are shown in Table 13. This apparently inherent tendency toward lack of apical dominance was characteristic of *floridanum* trees, and occurred in a significantly smaller percentage of other seedlings. The seedling characteristics evidently are similar to those of the parent trees; notes on the field labels describe *floridanum* as a comparatively small tree with poor form from

a timber standpoint. It seems, therefore, that this lack of apical dominance is a morphological character which is inherited and is not dependent on environmental conditions. The groupings shown in Figure 16 appear to be fairly distinct, with the exception of the inclusion of Tennessee trees in the southern groupings. Tennessee trees have a high percentage of "Type B" forking, but have many of the characteristics of northern trees.

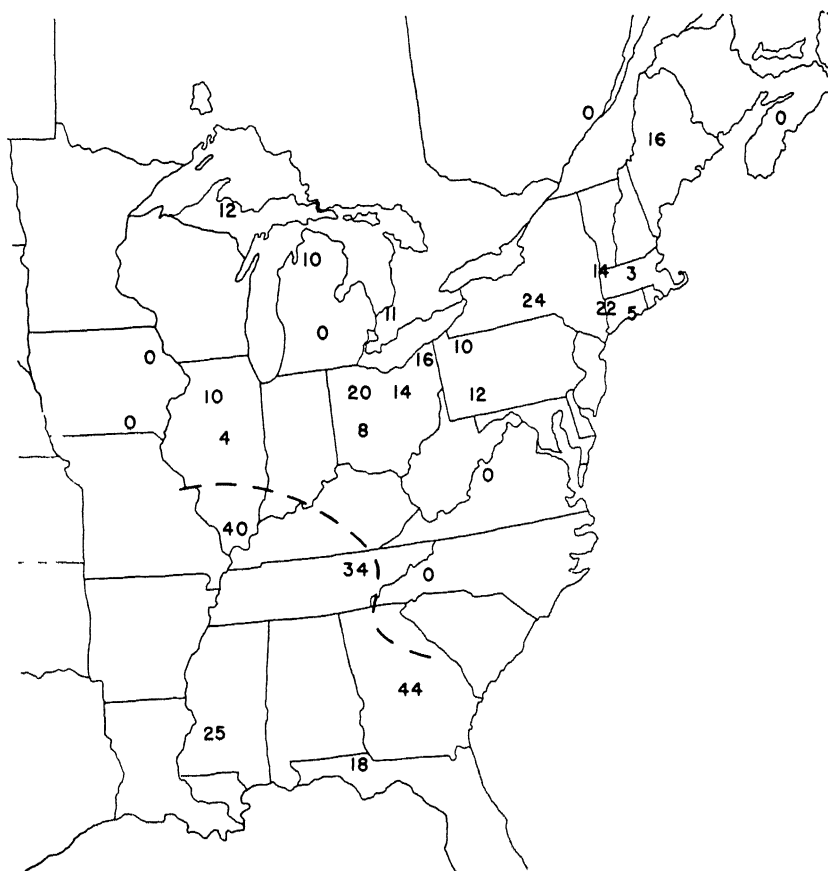


Fig. 20.—Percentage of trees with forking from causes other than shoot injury, with approximate ecotype boundaries. (Nursery trees.)

TABLE 13.—Regional variation in forking caused by conditions other than injury to shoot. Number of forked and unforked trees. Nursery, "A" subplots, 1955

Region	Number of sources	Forking Without Shoot Injury	
		Present	Absent
Northern and central	23	73	592
Southern (<i>floridanum</i>)	5	58	106

Chi square = 57.00***

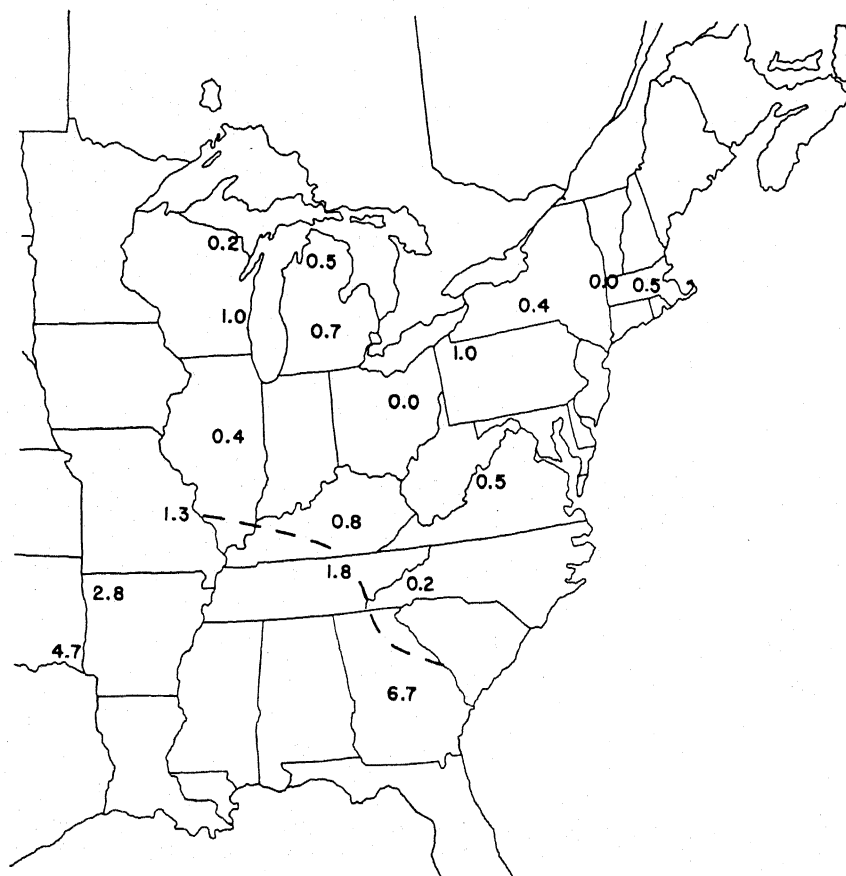


Fig. 21.—Number of forks per tree from causes other than shoot injury, with approximate ecotype boundaries. (Plantation trees.)

The same relationships were obtained from studies of the plantation trees. The average number of forks per tree was the basis of comparison, rather than the percentage of forked trees. Figure 21 presents the results of these measurements. The Missouri and Tennessee trees have some forking, but do not have the bushy appearance of Georgia and Oklahoma trees, and of some of the Arkansas trees. They may represent a transition form; there is considerable variation between individual trees, and those with foliage characteristics most nearly resembling *floridanum* are the trees with the most forking.

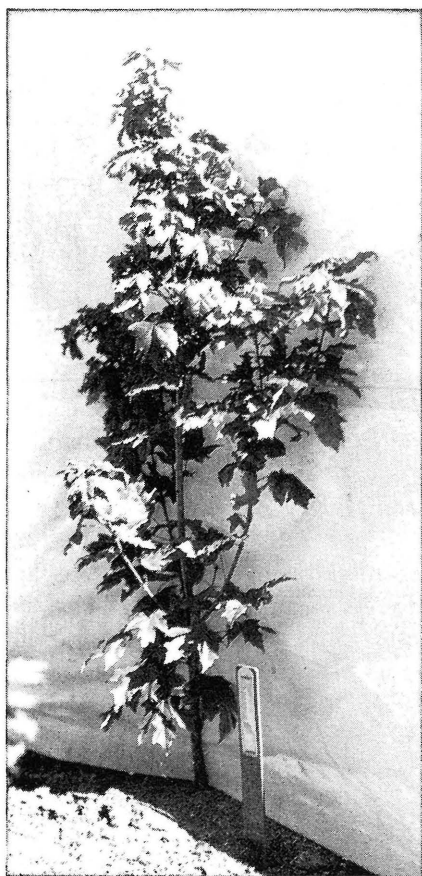


Fig. 22.—Form typical of trees of the southern ecotype.



Fig. 23.—Form typical of trees of the northern and central ecotypes.

The total pattern derived from both experimental areas is one of division into two morphological types, distinguished on the basis of degree of apical dominance. One form is represented by trees from the *floridanum* region, which have multiple stems, tending to create a bushy appearance (Figure 22). The other form is found in trees from northern and central regions; this type has a high degree of apical dominance (Figure 23). Evidence indicates at least partial discontinuity between the two types, although there is a possibility of some intergradation. Within the combined northern-central region, variation in time of shoot growth initiation produces variation in tree form, through the injurious effect of late spring frosts on early flushing trees. This differentiation was most evident between (a) trees from Canadian and northern Michigan sources and (b) trees from farther south. Trees from extreme southern sources also have this physiological sensitivity to frost, which increases the degree of forking at Wooster beyond that which would be caused by inherited lack of apical dominance.

Trees from the southern Appalachians had no forking, but this may be the indirect result of the small size of most of the trees. It is possible, on the other hand, that later study will show that trees from this region should be distinguished on the basis of a high degree of apical dominance.

Form Comparison of Black and Sugar Maple

The tabulated measurements suggested that source samples consisting entirely or predominantly of *nigrum* had less forking than *saccharum* trees. To test this statistically, the responses of individual *nigrum* progenies in the nursery were totalled, and the overall percentage of forking in *nigrum* trees was compared with the percentage of forking in *saccharum* trees within the range of black maple. Fisher's Exact Test was used (Fisher 1950, Mainland 1948). The results are given in Table 14. There was no difference in the percentage of forking resulting from the reaction to Wooster climate, but there was significantly less "inherent" forking in black maple. The black maple tested includes trees from Iowa, southern Michigan, Ohio, and Virginia. There was no indication that this was the effect of other conditions such as tree height. The results suggest that there may be a higher degree of apical dominance in *nigrum* than in *saccharum*, at least in the juvenile stage. The results are not conclusive, because relatively few sources of *nigrum* are represented. However, the sources are widely distributed throughout the range of black maple. This seems to be a difference which merits further study, because of its implications to the tree breeder who is interested in developing better timber types of sugar maple.

TABLE 14.—Number of forked and unforked trees of black and sugar maple, within the black maple range. Nursery, "A" subplots, 1955

	Number of sources	Forking due to winter injury		Forking not due to winter injury	
		Present	Absent	Present	Absent
Sugar maples in black maple region	18	73	441	77	437
Black maple	4	3	40	0	43
Probability that difference is due to chance		2P = 170		2P = 022	

Other Morphological Characteristics

LEAF OUTLINE

Approximately 1,400 measurements were taken of leaf shape, as a means of identifying the three subspecies.⁴ Figure 24 shows the subspecies most abundant among trees and herbarium specimens from each source. The map gives some indication of the ranges of *saccharum* and of *floridanum*, and zones of introgression. The range of *nigrum* is not shown, since it was not systematically sampled, although the predominance of *nigrum* in central and western Iowa is illustrated. The predominance of *nigrum* in southern Michigan however, is the result of deliberate sampling.

CHROMOSOME NUMBER

Chromosome counts were made of *saccharum* trees from Massachusetts, Ohio, and Tennessee, and of *floridanum* from Georgia. The results from several counts for each source were uniformly $2n = 26$. As far as can be determined, this is the first record of chromosome number in *floridanum*.

The genetic uniformity was expected, because most of the species in the genus *Acer* have been found only in the diploid condition, including sugar maple (*saccharum* and *nigrum*). In the present study, material from widely separated localities was examined, covering a large north-south distance and a wide variation in ecological conditions. There is no indication of polyploidy associated with geographic racial patterns, as Wright (1944) found in white ash.

⁴The numbering system is that used by Desmarais (1952) in his more extensive studies of leaf variation in *Acer saccharum*.

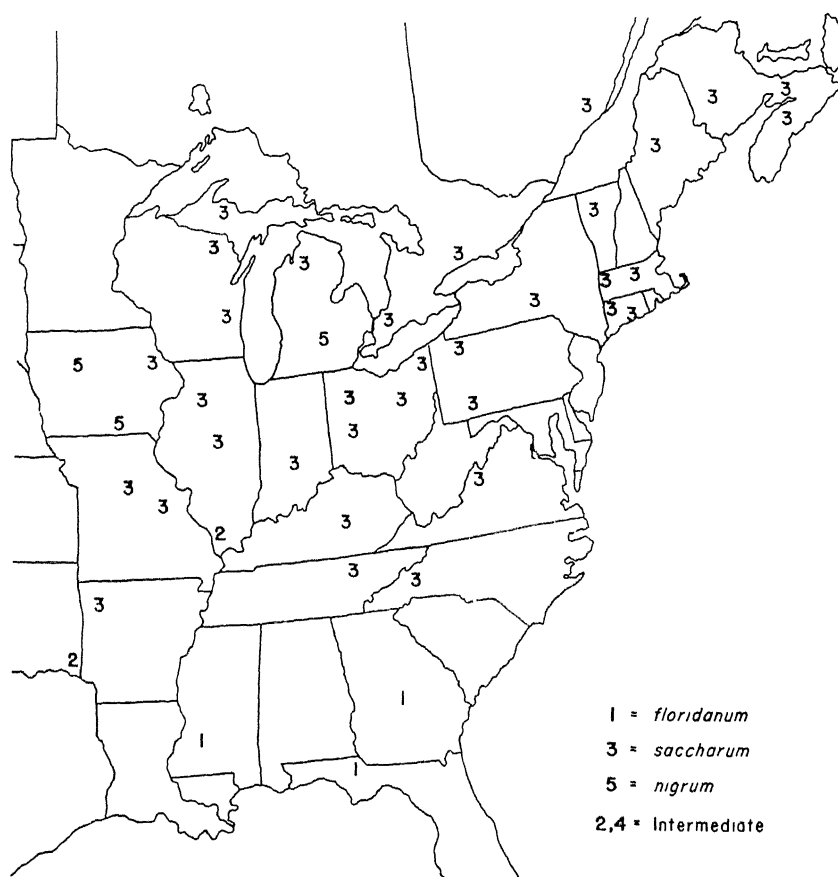


Fig. 24.—Leaf outline most abundant among trees from each source in the nursery and the plantation.

GROWTH RATE AND OTHER PHYSIOLOGICAL CHARACTERISTICS

Growth Rate

There was no indication of geographic variation in rate of height growth in the greenhouse, nursery, or plantation during 1954. The distributions of the values recorded appeared on inspection to be random, and no analyses were made. In October, 1955, the total height was measured of every tree in the nursery, to the nearest centimeter. An average value was then obtained for each subplot and a variance analysis was made. This analysis included the "A" subplots of fifteen

sources in Blocks II to V, omitting Block I because of its higher mortality and consequent poorer representation of some sources. Growth rate, being sensitive to environmental influence, could be studied most effectively by restricting analysis to sources represented by large numbers of seedlings.

The 1955 height growth measurements showed that there was significant variation caused by location in the nursery, but no significant difference associated with place of origin of the seed. Wide variation in height growth was common between individual trees in the same subplot, as illustrated in its extreme in Figure 25.

Height measurements taken at the end of the 1956 growing season again showed wide random variation. In the nursery there was greater height growth in *floridanum* trees than in northern trees. On the other hand, plantation measurements indicated that with increasing age these southern trees tend to have more and more of this total growth distributed over many stems, as a result of multiple forking.



Fig. 25.—Maximum extent of variation in height growth among nursery trees in the same subplot.

Other Physiological Responses

Several other physiological responses were studied. None of the differences seemed to be related to the source of the plant material. Germinative capacity of the *floridanum* seed may have been an exception; this seed germinated more rapidly and in higher total percentage than seed from other sources. However, precise comparison of germinative capacity of different provenances could not be made, because of unavoidable differences in length of cold storage period. The rapid germination of the *floridanum* seed may have been the result of a short required period of chilling, coupled with a long period of stratification.

Leaf color investigations did not show racial differences. Leaves of growing trees varied slightly in shade of green, but the tabulated data appeared to have a random pattern and no analysis was made. The bright red color common among developing leaves also had no apparent relation to source.

No differences were noted in resistance to insects or disease. Caterpillar damage to new leaves was common, but records indicated that selection was at random.

VARIATION IN RELATION TO THE ECOTYPE CONCEPT

The term "ecotype" was originally defined by Turesson (1922) as "the product arising as a result of the genotypical response of an eco-species or species to a particular habitat." Distinctness was considered to be one of the characteristics of an ecotype. However, it is possible that in many cases recognition of distinct ecotypes may be the result of insufficient sampling of intermediate populations. On the basis of available evidence, Gregor (1946) concluded that ecotypic variation is more often continuous than discontinuous. Stebbins (1950) recognized that clinal ecotypic variation may be prevalent where there is continuous variation of climate, although under other conditions there may be partial discontinuity in the variation pattern. Consequently, different species will vary in the ease with which distinct ecotypes can be recognized.

In the case of sugar maple, these studies provide evidence of continuous geographic variation in certain characteristics which are adaptive in origin, while other "adaptive" responses show sufficient discontinuity to permit recognition of ecotypes. In spite of variation within each ecotype, there is an appreciable degree of internal uniformity when one ecotype is compared with another. The transition zones between groupings are narrower in some regions than in others, because of the

varying influence of topographic and edaphic factors. Further local research is likely to clarify the nature of geographic variation in sugar maple. In the meantime, variation over the entire species may be grouped into three major geographic races or ecotypes, each containing parallel clinal variation which is part of a continental pattern.

CONCLUSIONS

1. From a physiological standpoint, as well as a taxonomic standpoint, sugar maple is best considered as a single species (*Acer saccharum* L.) There is a close interrelationship of physiological responses among the forms *saccharum*, *nigrum*, and *floridanum*.

2. Sugar maple has systematic patterns of geographic variation which can be explained by studying their relation to evolutionary influences. Some of the influences which have contributed to the differentiation of broad forest regions in eastern North America have also favored the development of fairly distinct genetic groups in sugar maple. The common characteristics of each group are adaptive in nature. On the other hand, certain environmental influences, day length, for example, have continuous geographic variation. Such conditions have, by the process of natural selection, produced clinal trends within the species. These two types of regional variation are superimposed; this is possible because one type of variation is found in responses which are compatible with, rather than exclusive of the other type.

3. Considering the range of the species, variation in winter-hardiness is not very great in sugar maple. Young trees from southern *floridanum* sources are sensitive to fall frost injury to the shoots, but most are able to withstand subzero temperatures without being killed. Trees from Canadian and northern United States sources are subject to moderate stem killing from late spring frosts because of their early time of bud-breaking in Ohio.

4. Sugar maple seedlings and young trees are sensitive to leaf injury under conditions of high insolation. There are three recognizable regional groupings, their distributions being closely associated with regional patterns of mean summer temperature. One group consists of subspecies *floridanum*; in Ohio these trees have little or no leaf injury of this type. Another group includes trees from the northern hardwood region, as defined by ecologists; these trees have the most leaf injury. The third group includes the remaining part of the species range; trees from this central region suffer moderate leaf injury. Within the central group, leaf injury appears to decrease in a clinal fashion from east to west.

5. There are at least two regional groupings in sugar maple differing in drought resistance. The most drought-resistant trees originate in central and southern regions. Trees from the northern hardwood region are more susceptible to drought. The geographic ranges of these two groups are not as clearly recognizable as they are in the case of leaf injury, probably because of the influence of local variation in soil moisture conditions. There is no difference in drought resistance between trees from the *floridanum* region and trees from the central region.

6. Variation in time of spring growth initiation is clinal; northern trees begin growth first at Wooster, followed by trees from regions to the south. At middle latitudes, development is most rapid among trees from the region just west of the Appalachians; Ohio valley trees leaf out ahead of trees from Appalachian and Illinois sources. Flushing occurs in trees from *floridanum* sources at about the same time as in Illinois trees. Photoperiod of source has some relation to the trend, and temperature may also be important. However, other evolutionary influences appear to have been more important. The shape of the trend on the map resembles the boundaries of Wisconsin and Illinoian glaciation in Ohio and Indiana. It is possible that a cooler climate during these periods in areas south of the glacial border may have favored the natural selection of northern genotypes in Kentucky and Tennessee.

7. The time at which trees stop putting out new stem growth varies between provenances. Trees from northern sources are the first to stop growing; trees from the Gulf Coastal Plain continue growth until killed back by frosts. The geographic pattern is not well-defined, however, and seems to be the result of a complex set of conditions. Temperature and day length have some relation to the response, but there are also other contributing conditions which are unknown.

8. The time of fall leaf coloration is subject to strong genetic control. Variation is continuous, beginning in northern trees and ending in southern trees. The time of leaf coloration is closely correlated with summer day length of the provenance. Summer temperature of the source modifies the trend, by slightly advancing the time of leaf coloration in trees from cool temperature regions.

9. Black maple trees (subspecies *nigrum*) cease height growth, develop fall leaf color, and lose leaves earlier than sugar maples (subspecies *saccharum*). Black maples from Iowa may be an exception; in trees from this region there was no evidence of phenological differences between *nigrum* and *saccharum*.

10. Variation in tree form among small sugar maples is the result of variation in the amount of forking. Two types of forking can be recognized: one is caused by frost injury to shoots; this represents a morphological expression of physiological variation, and is not found in the native locality. The other type apparently represents an inherent lack of apical dominance, and is not associated with shoot loss or injury. This second type of forking is very common among *floridanum* trees, but much less frequent among trees from all other sources.

11. There are indications that black maple has better form than sugar maple, at least in the seedling stage. Progenies of black maple from four widely distributed localities had significantly less forking of the "non-environmental" type than did sugar maples from the range of black maple. Further comparative study is needed of *nigrum* and *saccharum*.

12. There are no significant differences in growth rate between seedlings from different sources, at the end of three growing seasons and an initial period of growth in the greenhouse.

13. All these varying characteristics can be combined to give the total response of trees from any particular area. The genetic groupings or trends and their known characteristics are as follows:

(a) **Northern hardwood ecotype.** Trees of this ecotype may be either *saccharum* or *nigrum* (or intermediates). They are distinguished by relatively low genetic resistance to drought, susceptibility to leaf injury under high insolation, and high resistance to winter injury. At Wooster, trees from northern provenances in this ecotype are susceptible to slight injury from late spring frosts. There is a high degree of apical dominance.

(b) **Central ecotype.** Characteristics include high resistance to drought and moderately high resistance to leaf scorch, the latter increasing in a continuous trend from east to west. There is high resistance to winter injury, and a high degree of apical dominance. The race includes trees of subspecies *saccharum* and of subspecies *nigrum*.

(c) **Southern ecotype.** This grouping is identical with the subspecies *floridanum*. In addition to taxonomic features, other known characteristics include high resistance to drought and leaf scorch, moderately low resistance to winter injury, and poor form because of tendency toward repeated forking of the main and lateral shoots.

(d) Subspecies *nigrum* occupies parts of the northern hardwood and central ecotypes. The only distinguishing physiological characteristics found in this study are an earlier cessation of growth and indications of better form in young trees than is found in *saccharum*.

(e) At least two clines transect the ecotypes and have very little relation to their distributions. These include the cline in time of flushing, which "bulges" southward in the Ohio Valley, and the latitudinal cline in time of leaf coloration. As a result of these cross-patterns of genetic variation, there is wide differentiation in length of growing season within each ecotype. Consequently, there are a great many genotypic combinations of characteristics. The geographic locations of trees with a particular combination are predictable because they fit into a known, systematic arrangement.

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